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Landscape scale habitat suitability modelling of bats in the Western Ghats of India: Bats like something in their tea

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ABSTRACT

To conserve biodiversity it is imperative that we understand how different species respond to land use change, and determine the scales at which habitat changes affect species' persistence. We used habitat suitability models (HSMs) at spatial scales from 100–4000 m to address these concerns for bats in the Western Ghats of India, a biodiversity hotspot of global importance where the habitat requirements of bats are poorly understood. We used acoustic and capture data to build fine scale HSMs for ten species (*Hesperoptenus tickelli*, *Miniopterus fuliginosus*, *Miniopterus pusillus*, *Myotis horsfieldii*, *Pipistrellus ceylonicus*, *Megaderma spasma*, *Hipposideros pomona*, *Rhinolophus beddomei*, *Rhinolophus indorouxii* and *Rhinolophus lepidus*) in a tea-dominated landscape. Small (100–500 m) scale habitat variables (e.g. percentage tea plantation cover) and distances to habitat features (e.g. distance to water) were the strongest predictors of bat occurrence, likely due to their high mobility, which enables them to exploit even small or isolated foraging areas. Most species showed a positive response to coffee plantations grown under native shade and to forest fragments, but a negative response to more heavily modified tea plantations. Two species were never recorded in tea plantations. This is the first study of bats in tea plantations globally, and the first ecological Old World bat study to combine acoustic and capture data. Our results suggest that although bats respond negatively to tea plantations, tea-dominated landscapes that also contain forest fragments and shade coffee can nevertheless support many bat species.

1. Introduction

The need to protect and enhance the biodiversity potential of agricultural areas has become widely recognised (Daily, 2001; Daily et al., 2003; Perfecto et al., 2009; Mendenhall et al., 2014) as it becomes clear that even biodiversity in large habitat patches is not extinction proof if the patches are isolated (Ferraz et al., 2003). Furthermore, some of the major factors influencing biodiversity within protected areas are environmental changes occurring immediately outside them, often in agricultural landscapes (Laurance et al., 2012). Primary forest is irreplaceable (Gibson et al., 2011), but an agricultural landscape containing forest fragments and agroforestry plantations can support high biodiversity, help maintain viable populations of many species and increase resilience to a changing climate (Vandermeer and Perfecto, 2007; Sridhar et al., 2008; Mendenhall et al., 2014). However, species will differ in their ability to thrive in this matrix, so it is important to understand the extent to which each can use natural habitat patches of different sizes and different agricultural land uses, in order to manage habitats outside protected areas effectively (Melo et al., 2013).

Of all 35 biodiversity hotspots (www.conservation.org) in the world, the Western Ghats of India is the most densely populated by people (Cincotta et al., 2000). As a result, the natural vegetation in many places has been destroyed, degraded or fragmented, and only 6% of the land is currently under primary vegetation (Sloan et al., 2014). Large tracts of the Western Ghats are currently planted with tea, coffee, cardamom, eucalyptus and other crops, and much of the forest remains only as small fragments (Menon and Bawa, 1997; Bawa et al., 2007). However, even these fragments can support a high diversity of species, including endemic mammals, birds and herpetofauna as well as large predators and Asian elephants, most of which also use agricultural areas (Mudappa and Raman, 2007; Sridhar et al., 2008; Anand et al., 2010). The response of bats to forest fragmentation and land use change in the Western Ghats is poorly known, despite the importance of these species in ecosystems (Kunz et al., 2011).

This study investigated patterns of habitat use by an assemblage of bats in a predominantly agricultural landscape, the Valparai Plateau in the southern Western Ghats. The forest in this area was cleared and planted between 1900 and 1940, making it likely that much of the extinction debt has been paid (Cardillo et al., 2006). There are indications that bat assemblage structure and responses to habitat change in the palaeotropics are fundamentally different to those in the neotropics,

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but this may be confounded by a shorter history of forest clearance at many palaeotropical study sites (Heller and Volleth, 1995). Valparai has a longer history of clearance than several earlier palaeotropical studies, such as those in Malaysia, and is comparable with the dates of fragmentation at neotropical sites such as Barro Colorado Island, Panama.

Around 68% of Valparai is planted with tea. The area of India covered by tea plantations has doubled since the early 1960s (FAOSTAT, 2014) but the response of biodiversity to tea plantations has been little studied as they have been considered a 'green desert' (Daniels, 2003). About 11% of Valparai is planted with coffee, where *Coffea arabica* and *Coffea canephora* are grown under a mix of native rainforest shade trees and a few exotics. In India, the area planted with coffee has more than tripled since the early 1960s (FAOSTAT, 2014).

Few studies have taken a habitat suitability modelling (HSM) approach to tropical bats, and this is only the second HSM study of tropical bats built using acoustic data (Milne et al., 2006). It is also one of the few tropical bat HSMs to incorporate the effects of scale. Most tropical habitat suitability models for bats have been built with a cell size of 1–81 km^2 and analysed at a single scale (Milne et al., 2006; Lamb et al., 2008; Catullo et al., 2008; Hughes et al., 2012; Lee et al., 2012; Struebig et al., 2015). Some authors have suggested that as bats are mobile animals, fine scale factors are unlikely to drive occurrence patterns (Milne et al., 2006). Others have shown that precisely because of their mobility many bats can exploit small, isolated habitat resources and their occurrence is strongly driven by variables from scales as small as 20–500 m (Ober et al., 2008; Pinto and Keitt, 2008; Meyer and Kalko, 2008; Lookingbill et al., 2010; Bellamy et al., 2013; Hahn et al., 2014). An individual bat may respond strongly both to a small scale factor such as a small water body where it drinks or hunts, and simultaneously a larger scale factor such as the area of woodland across its home range that provides roosting sites; and bat species with different ecomorphologies may also operate predominantly at different scales (Gorresen et al., 2005; Pinto and Keitt, 2008; Bellamy et al., 2013).

We built HSMs using environmental data and habitat features quantified at multiple spatial scales for ten bat species, to identify the environmental variables driving their local distributions and to determine the scales at which environmental variables affect bats. In addition, we also quantified niche breadth and niche overlap within the bat assemblage and mapped predicted species richness in the landscape to identify areas of potential high bat diversity.

2. Materials and methods

2.1. Study site

The study was conducted in the Valparai plateau and adjacent Thalanar and Waterfall estates, in the state of Tamil Nadu in the southern Western Ghats, an area of approximately 485 km^2 (N 10.2–10.4°, E 76.8–77.0°; Fig. 1). The native vegetation is mid-elevation tropical wet evergreen forest of the *Cullenia exarillata–Mesua ferrea–Palaquium ellipticum* type (Pascal, 1988; Raman et al., 2009). The study site is an agricultural landscape dominated by tea plantations interspersed with shade grown coffee plantations, eucalyptus plantations, tropical rainforest fragments, streams, and riverine vegetation (Mudappa and Raman, 2007). The site is adjacent to the Anamalai Tiger Reserve in Tamil Nadu, Eravikulum National Park, Vazhachal Reserved Forest and Parambikulum Wildlife Sanctuary in Kerala. Elevation ranges from approximately 800–1600 m asl, and the average annual rainfall is 3500 mm, of which about 70% falls during the southwest monsoon (June–September) (Raman et al., 2009).

2.2. Bat data collection

Bats were sampled by capture at 43 sites and were recorded using Pettersson D240X time expansion bat detectors (www.batsound.com) on forty four 400 m long transects at 26 sites, and 2 km long transects at 18 sites. Data on the short transects were collected for direct habitat comparison (Wordley, 2014) while the long transects were designed to sample all habitats for HSMs, and to sample varying distances away from habitat 'edges'. Data from static direct sampling bat detectors (Pettersson D500X) at 38 locations were also incorporated into the bat HSMs. A handheld GPS (±3–10 m accuracy; Garmin GPSMaps 60 Cx, www.garmin.com) was used to record each sampling location. Capture and recording took place between late January and mid-May 2011, 2012, and 2013. For more detail see 'Bat Data Collection' section in Supporting Information.

As we wanted to map fine scale bat-habitat associations, we used fine scale data to build our models. Our data collection points on transects were 100 m apart, so we may have recorded the same bat on multiple points, leading to some degree of pseudoreplication. However, it is almost impossible to completely control for pseudoreplication when recording free ranging wild animals. The home range sizes for these bats and the degree of territorial overlap are for the most part totally unknown; so even if our survey points were 1 km apart some pseudoreplication could not be ruled out.

2.3. Call identification

Acoustic transect data were visualised as spectrograms to measure call parameters using BatSound (www.batsound.com). At each site, a species was marked as present if a call unambiguously attributable to that species was recorded. We modelled ten insectivorous species out of 15 insectivorous species recorded from this landscape and the adjacent Anamalai Tiger Reserve. The chosen species were clearly identifiable based on echolocation call characteristics, and recorded in five or more locations spread over more than 5 km^2 (Wordley et al., 2014; Wordley, 2014). The species we modelled exhibited variation in body size, wing aspect ratio and echolocation call frequencies, spanning the whole range of traits seen in insectivorous bats in the area (Wordley, 2014). Calls were identified using an echolocation call library developed for the area (Wordley et al., 2014).

2.4. Environmental data

In the absence of digital land-use data for the study area, we built a habitat map of the Valparai plateau and a surrounding 5 km buffer by manually classifying satellite imagery from Google Earth with subsequent ground verification using a GPS system (habitats listed in Fig. A1). The digital terrain model for the site was downloaded from https://earthdata.nasa.gov/user-mgmt/ at 92 m resolution. The map was built in ArcGIS 10.1.

GIS layers describing topography, habitat type and variables describing distance to a variety of resources and density of water features/woodland edge were created as rasters with a 50 m resolution. Further details are given in 'Environmental Data' section in Supporting Information. Apart from the non-scalar distance layers, all environmental variables were quantified at five different spatial scales (100 m, 200 m, 500 m, 1500 m and 4000 m). Scales were chosen based on the results of previous bat HSMs (Gorresen et al., 2005; Pinto and Keitt, 2008; Akasaka et al., 2010, 2012; Henry et al., 2010; Lundy et al., 2012; Bellamy et al., 2013).

2.5. Modelling

We followed the methods of recent work on bat Habitat Suitability Models (HSMs) to build the models as described by Bellamy et al. (2013). HSMs were created with MaxEnt Version 3.3.3 k (Phillips et al., 2006), using primarily default settings and one species record per 50 m cell. See 'Modelling' section in Supporting Information for

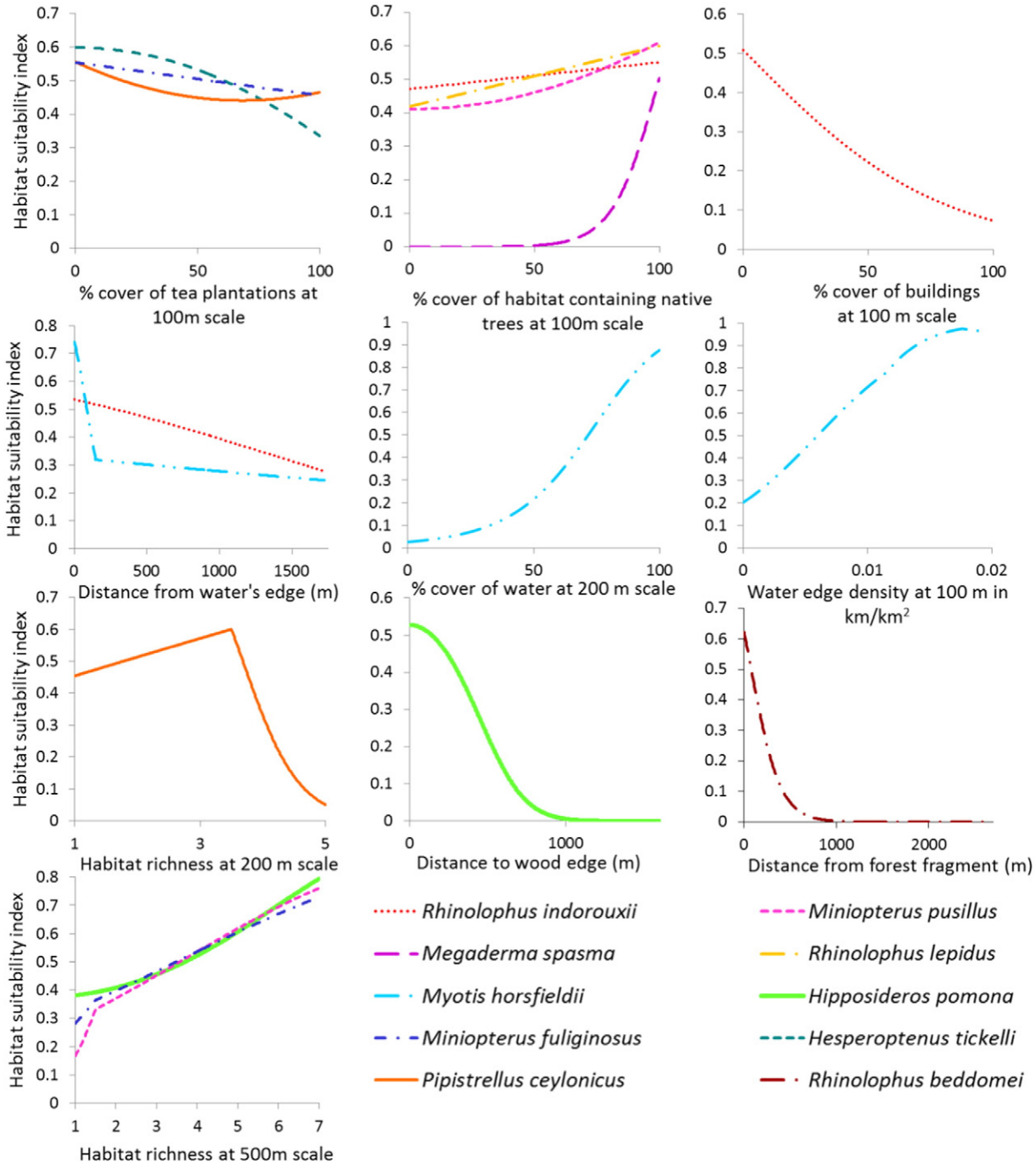

Fig. 1. The responses (habitat suitability) of each species to the habitat variables in their final model.

further details including a list of the environmental variables used (Table A2).

2.6. Sampling bias

In order to account for sampling bias, we created a bias file where the value of each 50 × 50 m cell represented the amount of time spent sampling in that cell, taking into account the different success rates of capture and acoustic methods. While we did not account for differences in species detectability, the main aim of the bias file was to distinguish sampled from unsampled areas. MaxEnt then corrects for non-uniform sampling effort (Dudík et al., 2005). We also used a mask file with 500 m buffers around every sampling site to constrain the pseudo-absence points to those buffers, to further reduce any effects of non-random sampling. See 'Modelling' in Supporting Information for further details.

2.7. Spatial autocorrelation

Residual spatial autocorrelation was controlled for by dividing the data into spatially clustered groups and testing models on data that were spatially independent of the training data (Parolo et al., 2008; Veloz, 2009; Bellamy et al., 2013). In this case, the study area was split into five roughly equal partitions and these were used for five-fold, spatially constrained cross-validation of every model. See 'Modelling' section in supporting information for further details.

2.8. Building multi-scale, multi-variate models

We built separate multi-scale, multi-variable predictive models for each bat species following the methods of Bellamy et al. (2013). For each species, we first independently assessed the predictive power of each of the 25 environmental variables considered in our study (Table A2) using the MaxEnt jackknife Area Under Curve (AUC) test statistic (see Bellamy et al., 2013). This included assessing the predictive power of each variable at each of the 5 different spatial scales (100 m, 200 m, 500 m, 1500 m and 4000 m) to identify the scale at which each variable best predicted species occurrence (highest test AUC). We discarded all variables that had poor predictive capabilities (AUC ≤ 0.5), and retained the remaining variables to create a 'full model' for each species that included both scalar and non-scalar variables at their best-performing scale. Within the full model, all variables were checked for multi-collinearity, and any pairs with a correlation of r ≥ 0.7 were identified using ENMTools (www.ENMTools.com, Fielding and Haworth, 1995; Warren et al., 2008). Where variables were correlated, the variable whose model had the lowest test AUC was removed. This left us with a subset of variables for each species that we called the 'subset model'. Pruned models perform better on independent test data, which suggests they may be less prone to over-fitting (Parolo et al., 2008; Bellamy et al., 2013).

To create models with the highest predictive power, the 'subset models' were further pruned to retain only the strongest predictors. Variables were removed in a jack-knife leave-one-out stepwise fashion to remove the variable with the lowest predictive power at each stage (Parolo et al., 2008). This process was repeated until only one variable remained. For each species, we then selected 3–9 models pruned from the 'subset model' that got comparable test AUC scores (Tables A3–A12); and for these models we also calculated the Akaike's Information Criterion corrected for small sample size (AICc). AICc was then used to identify the best models, and where this was inconclusive Log Likelihood and Bayesian Information Criterion (BIC) were used, all calculated in EMN tools (Warren and Seifert, 2011). See 'Model Selection' in Supporting Information for further details.

2.9. Niche breadth and overlap

Niche breadth is a measure of how much of the study landscape is suitable for each species. Niche breadth was quantified using the threshold independent inverse of Levin's metric in ENM tools (Levins, 1968; Warren et al., 2008), with higher scores indicating a larger area of the landscape used.

Niche overlap between species was measured in ENM tools using Schoener's D (Schoener, 1968), calculated as the difference in Habitat Suitability Index (HSI) between two species at each cell after the HSI map was standardised to sum to 1 over the entire study area (Warren et al., 2008). It ranges from 0 to 1, with zero indicating no niche overlap between species and one indicating identical predicted distributions.

2.10. Summed habitat suitability map

To create a map of the predicted species richness across the study area, we overlaid the continuous habitat suitability maps for each species, and summed the HSI across all species for each pixel.

3. Results

3.1. Scale

Scalar variables retained in the best performing models were mostly strongest at the 100 m scale, except percentage cover of water (200 m) and habitat richness (200–500 m) (Tables A3–A12, Fig. A2).

3.2. Species habitat responses

The strongest predictors for each species included both landscape composition variables such as 'tea plantation cover' and landscape configuration variables such as 'distance to water' (Table 1, Figs. 1 & 2). The extent of tea plantations in the surrounding landscape was an important predictor of habitat suitability for three species, with suitability declining in all cases with increasing cover of tea. The amount of native habitat in the neighbourhood was important for four species, with all showing a positive response. Water variables were most important for *Myotis horsfieldii*, which appears to be a riparian specialist, but distance to water also featured in the final model for *Rhinolophus indorouxii*, with both species declining away from water. Distance to forest fragments was the most important predictor for *Rhinolophus beddomei*, and distance to wood edge was important for *Hipposideros pomona*, with both species showing declines away from tree cover (Fig. 1). Four species showed positive responses to habitat richness of the surrounding landscape — this was the only variable strongest at the 500 m scale for any species. One of the final models had an AUC score >0.9, two scored >0.8, one 0.7, and the rest varied between 0.59 and 0.69 (Table 1). Models of 0.7 and above are generally considered to be of practical utility, however AUC is not always the best metric for evaluating models, and 'low' scoring models may still have some practical use (see 'Model Selection' in Supporting Information).

Table 1
Variables retained in the final models for each species, test AUC and niche breadth using Levin's metric.

Species	Variable	Scale	Response	Test AUC	Niche breadth
Hesperoptenus tickelli	Tea plantations	100 m	Negative	0.64	0.93
Miniopterus fuliginosus	Tea plantations	100 m	Negative	0.61	0.95
	Habitat richness	500 m	Positive		
Miniopterus pusillus	Habitat with native trees	100 m	Positive	0.7	0.93
	Habitat richness	500 m	Positive		
Myotis horsfieldii	Distance to water	NA	Negative	0.89	0.55
	Water	200 m	Positive		
	Water edge density	100 m	Positive		
Pipistrellus ceylonicus	Habitat richness	200 m	Positive	0.59	0.98
	Tea plantations	100 m	Negative		
Megaderma spasma	Habitat with native trees	100 m	Positive	0.88	0.22
Hipposideros pomona	Distance to wood edge	NA	Negative	0.67	0.9
	Habitat richness	500 m	Positive		
Rhinolophus beddomei	Distance to forest fragments	NA	Negative	0.92	0.4
Rhinolophus indorouxii	Buildings	100 m	Negative	0.65	0.98
	Habitat with native trees	100 m	Positive		
	Distance to water	NA	Negative		0.93
Rhinolophus lepidus	Habitat with native trees	100 m	Positive	0.69	

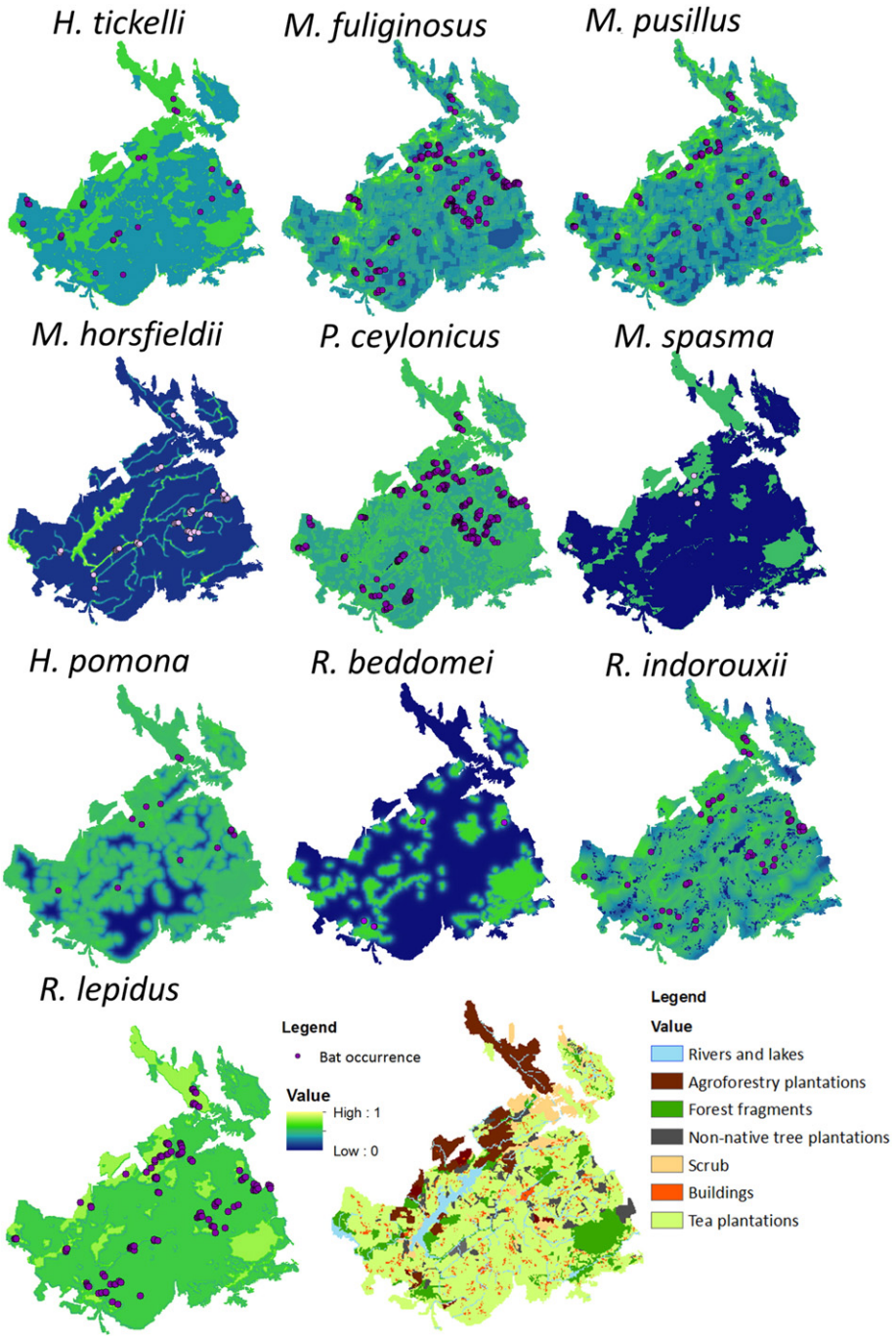

Fig. 2. Maps of predicted habitat suitability of each species across the study area, with actual occurrence points marked. The habitat suitability index ranges from 0 to 1.

3.3. Niche breadth and overlap

All the species had broad niches >0.9, with three exceptions; *M.horsfieldii*, *Megaderma spasma* and *R.beddomei* (Table 1). Schoener's D statistic showed *M. spasma* and *R. beddomei* to have the least niche overlap with other species (*M. spasma* 0.2–0.37, *R. beddomei* 0.37–0.53, Table 2). *M. horsfieldii* had the next lowest overall niche overlap with other species (0.2–0.7). Niche overlap between all the other species was high (>0.8).

3.4. Overall habitat richness map

The map of summed habitat suitability across all species (Fig. 3) shows high predicted species richness in forest fragments, agroforestry plantations and along rivers, and low predicted richness in areas dominated by tea plantations (compare Figs. 3 and A1). In tea plantation areas with nearby forest/agroforestry patches and rivers (especially those bordered with riparian vegetation) predicted richness is greater than in areas (such as in the south-west of the study area), where there are fewer patches of habitat containing native trees. Riparian vegetation is predicted to be especially rich.

4. Discussion

4.1. Scale

For all species the scalar variables (with the exception of habitat richness) in the final model showed the highest predictive power at

Table 2
Niche overlap using Schoener's D statistic. Darker colours indicate greater niche overlap between species.

D statistic	*H. pomona*	*R. indorouxii*	*H. tickelli*	*M. spasma*	*M. fuliginosus*	*M. pusillus*	*M. horsfieldii*	*P. ceylonicus*	*R. beddomei*	*R. lepidus*
H. pomona		0.859	0.855	0.270	0.884	0.889	0.648	0.893	0.527	0.884
R. indorouxii			0.863	0.275	0.873	0.875	0.689	0.887	0.481	0.897
H. tickelli				0.308	0.877	0.894	0.691	0.901	0.481	0.918
M. spasma					0.240	0.292	0.203	0.252	0.371	0.289
M. fuliginosus						0.935	0.700	0.915	0.485	0.908
M. pusillus							0.689	0.900	0.501	0.915
M. horsfieldii								0.698	0.408	0.686
P. ceylonicus									0.474	0.934
R. beddomei										0.487
R. lepidus										

100–200 m scales. This probably reflects the mobility of bats: they can exploit small patches of scattered resources, and often have small foraging 'beats' (Senior et al., 2005). Bat–habitat associations at small scales probably reflect decisions made by bats on where exactly to feed within their larger home range (Bellamy et al., 2013).

4.2. Model performance

Model performance based on AUC values was greater for the more specialist species with a smaller niche breadth (*M.spasma*, *R.beddomei*, and *M.horsfieldii*; AUC > 0.8 all cases) than for the species using a greater proportion of the landscape (AUC for all other species ≤0.7; see 'Model Selection' in Supporting Information). *M.spasma* and *R.beddomei* were both restricted to habitats containing native trees. *M.horsfieldii* was only found over rivers, indicating that it is probably a water specialist

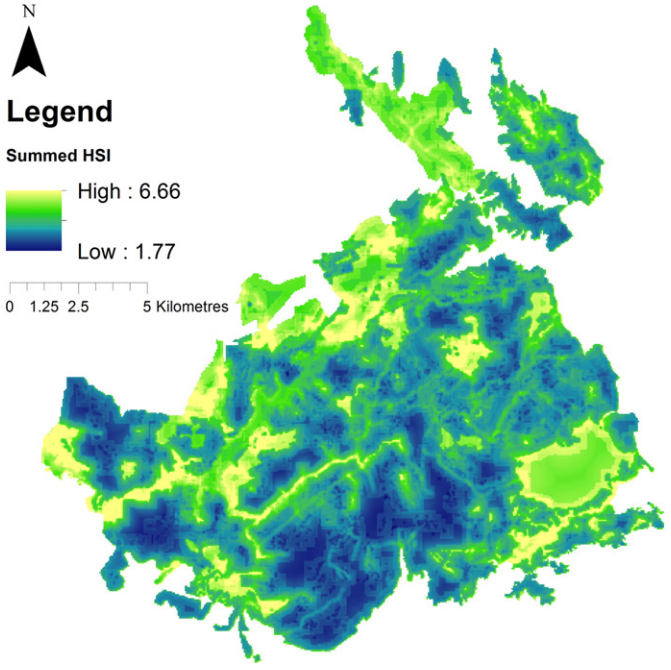

Fig. 3. Predicted species richness across the study landscape based on summed habitat suitability index scores.

like *Myotis daubentonii* (Senior et al., 2005). Lobo et al. (2008) demonstrated that smaller the ratio of the extent of occurrence of a species to the extent of the study area, the more accurate a HSM is likely to be, because it is more likely that pseudo-absence data will be environmentally distinct from presence data. Generalist species have weaker associations with most environmental variables as they can exploit many habitats, so low AUC scores are to be expected at the small scale of this study where the entire area falls within the latitudinal and altitudinal range of the study species. However, patterns of occurrence of generalist species can still be useful for land management decision-making. The use of the mask and bias file reduce spurious correlations caused by sampling habitats in different proportions to their prevalence in the landscape. We accounted to some degree for differing detectability between methods in our bias file; a further approach could be to calculate likelihood of detection per species, habitat and method used. However, this may not improve model performance greatly, as even simply scoring a cell each time it was sampled by acoustic or catching methods significantly reduced overfitting (Bellamy et al., 2013).

4.3. Niche breadth

Most of the species studied overlap greatly in their niches and use much of the available landscape. The exceptions are *M.spasma*, *R.beddomei*, and *M.horsfieldii*, which have narrower niche breadths and less overlap with other species. A larger scale study, encompassing greater habitat, topographical and climatic changes, may produce different results in terms of niche breadth and overlap.

4.4. Conservation implications

As many of the species responded similarly to many environmental variables, habitat management decisions have the potential to affect most, not just a few, species. For most of the species modelled here, agroforestry plantations and forest fragments appeared to offer similar benefits. *M.spasma* and *R.beddomei* are the species most at risk from the loss of forest fragments and agroforestry plantations as they were never recorded in tea plantations. Both species show traits associated with forest dependence in bats, such as low wing aspect ratio and low wing loading (Norberg and Rayner, 1987; Wordley, 2014). *M. spasma* and *R. beddomei* are thus likely to be at risk of decline from deforestation across Asia. This is supported by Struebig et al. (2008), who found *M. spasma* and *Rhinolophus luctus* (related to *R. beddomei*) to be rare in a fragmented landscape, and Struebig et al. (2015) who found that forested habitats were highly suitable for *M. spasma* and *R. luctus*, but that plantations and croplands were not.

Even a 2.2 ha forest fragment held at least six of the species studied, including *M.spasma*. Very mobile vertebrates such as bats and birds often seem to be able to use small habitat patches (Faria, 2006; Meyer and Kalko, 2008), and this study supports that. This is encouraging for conservation efforts in the area by the Nature Conservation Foundation (ncf-india.org), which have focussed on restoring and extending small, degraded forest fragments. A recent meta-analysis found that forest fragment size affected bat richness in a lake-island system, but that in a countryside system where the matrix was agroforestry and pasture, the effect often disappeared (Mendenhall et al., 2014). However, several species show reductions in genetic diversity with reduced fragment size (Struebig et al., 2011), and species richness may mask changes in species composition from intact forest (Cosson et al., 1999; Struebig et al., 2008, 2009; Estrada-Villegas et al., 2010).

This paper supports studies from the neotropics suggesting that shade coffee can provide a good habitat for many bat species (Pineda et al., 2005; Faria, 2006; Harvey and Villalobos, 2007; Pardini et al., 2009; Williams-Guillén and Perfecto, 2011). Of the two palaeotropical studies, one in Indonesia (based on capture) found richer bat assemblages in shade coffee than in forest (Graf, 2010). The other used acoustic transects in India but could only identify bats to family level —

activity was higher in forest fragments than in coffee (Molur and Singh, 2009).

The summed HSI map showed riparian areas to have high predicted species richness, even in tea plantations, but especially where there were native trees along river banks. A focus on improving native tree cover in riparian areas will benefit many bat species. Riparian ecosystems are known to be important for many bat species as they provide water to drink, insect food and different plant resources when compared to dry forest, as well as open flyways (Fukui et al., 2006). In temperate regions, riparian vegetation has been positively correlated with bat activity (Ober et al., 2008; Lundy and Montgomery, 2009). Milne et al. (2006) linked the positive effect on bats of habitat richness with their use of riparian areas, which may also hold true in this study. The use of forest edge habitats by some species may also drive the link between habitat richness and bat activity.

Seven species were recorded in tea plantations, and *M.horsfieldii* was recorded over rivers with tea planted up to the banks. Given that most of the species documented in tea plantations also had positive associations with habitat containing native trees, habitat richness or distance to wood edge in their final model, it seems that these species require adequate native tree cover in the landscape to persist. For example, where *H. pomona* was found in tea plantations it was within 350 m of wooded habitat and sometimes also over a river. Tea plantations are a poorer habitat for bats than coffee plantations, supporting studies on birds and frogs that show a reduction in species richness and changes in species composition in tea plantations compared to shaded coffee plantations and forest fragments (Raman, 2001; Murali and Raman, 2012). In ecologically important areas such as the Western Ghats it would be beneficial to biodiversity to prevent further conversion of shade plantations to tea, and to restore and plant forest fragments and riparian corridors. The value of tea plantations for biodiversity could potentially be enhanced by the use of native trees instead of silver oak for shade.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2015.08.005.

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